1   Seabird colony effects on soil properties and vegetation zonation patterns on King George

2   Island, Maritime Antarctic

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15   ABSTRACT

16   Seabirds are amongst the most important vectors transferring biogenic compounds from the

17   sea onto land in the polar regions and, consequently, influencing the properties of soil and

18   <mark>vegetation</mark>. We studied the influence of bird colonies (Adélie and gentoo penguins, giant

19   petrels), on soil properties and plant communities on King George Island, Maritime Antarctic.

20   We designated seven transects, each starting from the colony edge and running to a natural

21   boundary feature, which were divided into contiguous sample plots where we identified

22   specific plant taxa (*Prasiola crispa, Deschampsia antarctica, Colobanthus quitensis, Usnea*

23   sp.), as well as hydrophilous and xerophilous ecological groups of mosses. Based on

24   percentage contributions of each of these taxa, we distinguished six distinct vegetation zones

25   along the transects, in which we measured physical (moisture, conductivity and pH) and

26   chemical (NO_3^-, NO_2^-, NH_4^+, K^+ and PO_4^{3-} content) soil parameters. Our study confirmed that,

27   with increasing distance from bird colonies, the concentration of nutrients and soil

28   conductivity decreased, while pH increased. The vegetation zones were clearly related to this

29   gradient of seabird colony influence, and occurred in the same sequence for all three bird

30   species examined, although the largest colony of Adélie penguins had the strongest effect on

31   vegetation. Similarly, the physical and chemical soil properties did not differ significantly

32   between the colonies.

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34   Keywords: vegetation zones, soil chemistry, environmental gradient, penguins, petrels

Introduction

Polar terrestrial ecosystems are defined as subsidiary because they depend largely on marine-derived nutrients (Odum 1989). Marine birds and mammals, which forage in the sea and reproduce on land, are amongst the most important vectors transferring biogenic compounds and organic material from the sea to land (Smith and Froneman 2008). Seabirds introduce these materials to the terrestrial food-web through their carcasses, dead chicks and eggshells, food scraps, feathers and guano, and they consequently influence the properties of soil and vegetation (Stempniewicz 1990, 2005; Sun et al. 2002, Bokhorst et al. 2007; Stempniewicz et al. 2007; Zhu et al. 2013, Zwolicki et al. 2013; Ziółek and Melke 2014).

In Antarctic terrestrial ecosystems nutrient availability and turnover are limited by low metabolic activity and low rates of primary production, which result from the short growing season and chronically low summer temperatures (Smith 1984). Vegetation develops on typically small ice-free areas, including those recently uncovered by glacier retreat (Cook et al. 2005; Convey and Smith 2006). The 'Antarctic herb tundra formation', one of the most widespread vegetation types in the maritime Antarctic, comprises mostly mosses and lichens and includes only two indigenous species of vascular plants, the grass *Deschampsia antarctica* Desv. (Poaceae) and the pearlwort *Colobanthus quitensis* (Knuth) Bartl. (Cariophyllaceae) (Greene and Holtom 1971; Smith 1972; Longton 1988; Alberdi et al. 2002).

Antarctic vegetation communities often develop in sites enriched by seabirds or marine mammals (Ryan and Watkins 1989; Smith and Froneman 2008), although this feature has perhaps been noted more widely and impressively in the High Arctic (Odasz 1994; Croll 2005; Zmudczyńska et al. 2009, 2013). Recently, changes have been recorded in the composition and abundance of avifaunal communities in the South Shetland Islands, especially decreases in penguin population numbers (Ciaputa and Sierakowski 1999;

60   Korczak-Abshire 2010). These changes may, therefore, significantly impact vegetation

61   community structure and function. Areas that have been abandoned by penguins are rapidly

62   colonized by complex plant formations, facilitated by both the considerable nutrient resources

63   and the cessation of trampling by the birds (Tatur et al. 1997; Emslie et al. 1998; Juchnowicz-

64   Bierbasz and Rakusa-Suszczewski 2002).

65   The significance of the large amounts of nutrients supplied by breeding birds has been

66   recognized in many studies (eg. V. Smith 1978; R.I.L Smith 1984; Tatur and Myrcha 1984;

67   Ryan et al. 1989; Myrcha and Tatur 1991; Hovenden and Seppelt 1995). Tatur (2002)

68   calculated that the 30–50000 pairs of *Pygoscelis* genus penguins nesting on the west side of

69   Admiralty Bay (King George Island) deposited about 6.35 tonnes of guano per day, equating

70   to up to 10 kg of dry excreta per square meter of colony area during the breeding season. The

71   impact of this fertilization is manifested particularly in the vegetation composition, diversity

72   and abundance. Various studies have reported zonation of vegetation around nesting areas and

73   colonies (Smith 1984; Zarzycki 1993; Olech 2002), in particular recognising the balance

74   between increased plant diversity and growth rate associated with nutrient enrichment, and

75   limitation of growth caused through both intense trampling and levels of fertilization

76   exceeding those that can be tolerated by plants close to the colony (e.g. Smykla et al. 2007).

77   However, as yet, no attempt has been made to quantify physical and chemical soil conditions

78   underlying these vegetation patterns in the Antarctic.

79   Well-documented environmental changes, such as warming of the atmosphere and

80   ocean around Antarctica resulting in melting of perennial snow, retreat of glaciers and

81   reduced sea ice cover have taken place over recent decades and may change ecosystem

82   structure and function in the maritime Antarctic (Convey et al. 2009; Chwedorzewska 2009;

83   Turner et al. 2009, 2013, 2014; Convey 2011). Therefore, this study set out to describe the

84   relationships between the physical and chemical properties of the soil and the development of

85   specific vegetation zones. We tested hypotheses that the development of particular plant

86   communities in the vicinity of seabird colonies is determined by: (1) nutrient composition, (2)

87   nutrient concentration, and (3) colony type and species of seabird involved.

88

89   Materials and methods

90   *Study Area*

91   The study was conducted on King George Island (South Shetland Islands) during

92   two expeditions from December 2005 to January 2006 and from December 2006 to January

93   2007 (Fig. 1). The study area was located in Antarctic Specially Protected Area 128 Ecology

94   Glacier in the vicinity of the Polish Henryk Arctowski Antarctic Station. King George Island

95   (61°50'–62°15'S, 57°30'–59°01'W), is the largest of South Shetland Islands archipelago,

96   located 160 km from the Antarctic Peninsula, from which it is separated by the Bransfield

97   Strait. The average annual temperature is 1.7°C. As is typical of the maritime Antarctic

98   region, the island experiences a strong oceanic influence, with high humidity (84%) and

99   considerable precipitation. It also exposed to strong winds that often reach hurricane force

100   (Walton 1984; Convey 2013).

101   Notwithstanding the generally extreme environmental conditions, ice-free areas,

102   constituting less than 10% of the island's area, host relatively well developed terrestrial

103   ecosystems. King George Island, and in particular the western coast of Admiralty Bay, is one

104   of the richest botanical areas both of the maritime Antarctic biogeographical region and of the

105   entire Antarctic continent (Rakusa-Suszczewski 2003; Krzewicka and Smykla 2004). The

106   island's vegetation is composed mainly of mosses, lichens, algae and cyanobacteria. Vascular

107   plants are represented by two species, the Antarctic hair grass *D. antarctica* (Poaceae) and

108   Antarctic pearlwort *C. quitensis* (Caryophyllaceae) (Smykla et al. 2007).

109   In general, vegetation development is concentrated in coastal areas, particularly close

110   to those where marine birds and mammals breed and/or rest in high numbers. The most

111   numerous vertebrate in the study area is the Adélie penguin (*Pygoscelis adeliae*, c. 15,000

112   breeding pairs), with other species represented by much smaller populations - gentoo penguin

113   (*P. papua*, 30 pairs), kelp gull (*Larus dominicanus*, 40 pairs), southern giant petrel

114   (*Macronectes giganteus*, 11 pairs), Brown skua (*Stercorarius antarcticus* ssp. *lonnbergi*, 225

115   pairs). Marine mammals, including the southern elephant seal (*Mirounga leonina*) and

116   Antarctic fur seal (*Arctocephalus gazella*), also contribute to enrichment of the terrestrial

117   ecosystem, while rapidly expanding regional populations of the latter have led to considerable

118   damage and loss by trampling and over-fertilisation of large areas of maritime Antarctic

119   terrestrial vegetation (Favero-Longo et al. 2012).

120

121   *Collection of vegetation data*

122   Data were collected in areas influenced by Adélie penguin, gentoo penguin and

123   southern giant petrel colonies. Seven transects were designated on topographically similar

124   profiles, each 1 m wide and ranging from 60 to 120 m in length, starting from the colony edge

125   and running down the slope to a natural boundary feature, such as a stream, a small water

126   body or the seashore. Three transects were defined close to an Adélie penguin colony, two

127   from a southern giant petrel colony and two from a gentoo penguin colony (Fig. 1). Each

128   transect was subdivided into contiguous sample plots (1×1 m), meaning that they included 60

129   to 120 sample plots depending on their length, and the study included a total of 568 plots.

130   Within all sampling plots along each transect we identified four specific taxa: *P.*

131   *crispa, D. antarctica, C. quitensis* and *Usnea* sp., and additionally determined two ecological

132   groups of mosses, hydrophilous (predominantly *Sanionia georgico-uncinata*) and xerophilous

133   (including *Polytrichastrum alpinum, Syntrichia saxicola, S. princeps* and *Polytrichum*

134   *piliferum*), and visually assessed their percentage contribution to total vegetation cover.

135

136   *Physicochemical analysis of the soil*

137   Sample plot selection for chemical analyses was determined on the basis of gradient

138   analysis of vegetation (see below) using the first DCA axis for each transect separately. The

139   plots with highest response of a given taxon/ecological group, as assessed by the highest

140   percentage cover, were chosen for chemical sampling. The total number of soil samples

141   collected for physical and chemical analyses was 72. Three samples of the surface layer of

142   soil were collected from each of the plots (representing the five zones distinguished by the

143   TWINSPAN classification on each of the six transects) from points lying on the same

144   diagonal of each sampling plot (one from the centre and two from the corners of the plot).

145   Samples were taken from the soil surface layer using a metal cylinder (diameter = 5 cm) to a

146   depth of 10 cm. Each soil sample was separated into three subsamples of c. 80 cm^3, weighed

147   to the nearest 0.1 g, and subjected to further analyses in order to assess:

148   1) Soil moisture [%] – by weighing a subsample before and after oven drying (120°C) to

149   constant mass.

150   2) Soil conductivity (μS cm^{-1}) and pH – samples of 80 cm^3 were mixed with 160 cm^3 of

151   distilled water. The solution was shaken for ca. 20 min and then filtered through a

152   sieve (0.5 mm diameter mesh). The conductivity and pH were quantified in the filtrate

153   using a pH/conductivity/salinity meter CPC-401 (Elmetron).

154   3) Soil nitrogen (NO$_3^-$, NO$_2^-$ and NH$_4^+$), potassium (K$^+$) and phosphate (PO$_4^{3-}$) content

155   (mg 1000 g^{-1} soil dry mass) – samples of 80 cm^3 were mixed with 200 cm^3 0.03 N

156   acetic acid. Closed vessels were left for ca. 60 min and shaken regularly. The solution

157   was centrifuged for 15 min at 2500 rpm and filtered first through a sieve (0.5 cm

158   diameter mesh) and then through filter paper (MN 640 w, Macherey–Nagel diameter =

159   125 μm). Filtrates were analyzed using a photometer LF205 following standard

160   procedures (Cygański 1994).

161

162   *Data management and statistical procedures*

163   Detrended Correspondence Analysis (DCA, unimodal gradient analysis) was

164   performed to ordinate the vegetation plots and used to define plot selection for chemical and

165   physical sampling (ter Braak and Smilauer 2012). Vegetation zone classification was

166   performed using the TWINSPAN method under the following conditions: 6 cut levels: 0, 2, 5,

167   10, 20, 50 (%); minimum 5 samples by group size for a division, and maximum 7 indicators

168   per division (TWINSPAN for Windows 2.3) (Hill and Šmilauer 2005). Differences between

169   separate groups of vegetation and soil chemistry samples were examined using ANOSIM

170   (analysis of similarities, with Monte Carlo permutation test) with one-way and two-way cross

171   and nested comparisons design. Data standardization was performed only for physical and

172   chemical variables. In order to illustrate the level of similarity between the identified

173   vegetation zones and seabird colony types, a non-metric multidimensional scaling (MDS) was

174   applied on the matrix of Euclidean distances between samples. These analyses were run on

175   the log-transformed data [$x'= \log (x + 1)$]. Additionally, similarity percentages analysis

176   (SIMPER) was used to define the contribution of each taxon/ecological group to

177   dissimilarities between the distinguished groups. ANOSIM, MDS and SIMPER were run in

178   Primer 6.1.5. (Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Warwick 1994). For

179   each of the physical and chemical soil parameters we conducted comparisons between the

180   identified vegetation zones using non-parametric Kruskal-Wallis and *post hoc* Dunn tests

181   using the STATISTICA 9.0 package (StatSoft, Inc. 2010).

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186   Results

187   *Vegetation analysis*

188   On the basis of the TWINSPAN classification we separated six distinct vegetation

189   zones along the transects. These were, starting from the colony edge:

190   1) *Prasiola crispa* zone (P) with *P. crispa* 100% relative ground cover, 2) *D. antarctica* and

191   *P. crispa* zone (PD) – *P. crispa* 41% and *D. antarctica* 59% relative cover, 3) *D. antarctica*

192   zone (D) – monospecific occurrence of Antarctic hair grass, with 64% relative cover, 4)

193   mosses and *D. antarctica* (MD) –56% relative cover of hydrophilous mosses, with 25% cover

194   of Antarctic hair grass, 5) mosses and lichens (ML) – mixed xerophilous moss community

195   with relative cover of 31%, and the highest relative cover values recorded for macro lichens

196   (*Usnea* sp. 7.5%) and *C. quitensis* (13%). Finally, we also defined a trampled (T) zone –

197   including areas trampled by the birds and temporary ponds or puddles. Sampling plots

198   included in this zone were present across the different zones in all transects, and are not

199   included in the subsequent analyses. Percentage cover values and frequencies of occurrence of

200   individual taxa are shown in Table 1.

201   Analysis of similarity between groups identified using TWINSPAN confirmed that

202   they were distinct and that their membership was non-random (ANOSIM One-Way Analysis,

203   Global Test; $R = 0.79$ p = 0.001). Pairwise comparisons confirmed that all the zones differed

204   significantly (p = 0.001) (Fig. 3).

205   *Soil physical and chemical characteristics in vegetation zones*

206   Within the transects, the vegetation zones differed in terms of their overall

207   physicochemical parameters (ANOSIM Two-Way Crossed Analysis, Global Test; $R = 0.13$

208 p = 0.001). Detailed comparisons for each of the physical and chemical soil properties

209 revealed significant differences between the zones (all Kruskal-Wallis tests, p < 0.001,

210 differences in *post hoc* tests p < 0.01).

211 Starting from the colony edge, clear gradients of measured ion concentrations and soil

212 conductivity could be seen, with the highest values in the P zone and decreases through the

213 successive zones (form P to ML; Fig. 4, Table 2). The P zone demonstrated the highest

214 number of significant differences in terms of physical and chemical soil parameters in

215 comparison with other zones. No significant differences were found between PD and D zones

216 in any of the measured parameters. A distinct gradient was present in pH, which increased

217 with progression from the colony edge and was significantly higher in the final ML zone than

218 in other zones. The ML zone also had the lowest soil moisture values, differing significantly

219 from all other groups except the P zone (Fig. 4g, Table 2).

220

221 *Influence of seabird species on vegetation zonation*

222 Similarity analysis revealed no significant differences between the three bird species in

223 physical and chemical properties of soil measured within the identified vegetation zones

224 (ANOSIM Two-Way Nested Analysis, Global Test $R = 0.22$ p $= 0.72$). Plant species

225 composition within each of the five zones was also similar between the bird species

226 (ANOSIM Two-Way Nested Analysis, Global Test $R = 0.13$, p $= 0.16$).

227 Two-Way Crossed Analysis, testing for differences between colony types regardless

228 of any differences between the vegetation zones, revealed no significant differences in soil

229 characteristics (ANOSIM Two-Way Crossed Analysis, Global Test; $R = 0.06$ p $= 0.11$).

230 However, the transects near the Adélie penguin colony differed significantly from those

231 associated with the other two bird species (ANOSIM, Two-Way Crossed Analysis Global

232 Test; $R = 0.16$ p $= 0.001$, Pairwise Tests p < 0.01). MDS analysis (Fig. 3) confirmed that

233   samples from the Adélie penguin transect did not share exactly the same similarity space as

234   those from the other colonies. The main differences were among plots from the first three

235   zones dominated by *P. crispa* and *D. antarctica* (P, PD, D). However, gentoo penguin and

236   petrel colonies differed from Adélie mainly due to the samples from the final zone along the

237   transect (ML) (Fig. 3). SIMPER analysis revealed average dissimilarities in vegetation

238   composition between the Adélie and gentoo penguin transects of 53.9%, and between Adélie

239   and giant petrel transects of 50.7% (Table 3). The Adélie penguin transect was characterized

240   by substantially lower mean cover of hydrophilous mosses, contributing 47.1% of

241   dissimilarity in comparison with the giant petrel transect and 19.1% with the gentoo penguin

242   transect. The next largest contribution to differences between colony types was due to the

243   presence of *D. antarctica,* whose average cover was greater on the giant petrel and gentoo

244   penguin transects. Of the three bird species examined, the Adélie penguin transect was

245   characterized by the largest cover of the alga *P. crispa*, which was the third most important

246   contributor to dissimilarity between transects. Xerophilous mosses, *C. quitensis* and *Usnea* sp.

247   were of minor importance in the differentiation between colony types (Table 3).

248

249   Discussion

250   In polar regions, vegetation patterns have been variously associated with proglacial

251   chronosequences, topographical gradients (Frenot et al. 1998; Kojima 2002; Ohtsuka et al.

252   2006), and environmental gradients created by seabirds, with the latter having perhaps the

253   most striking influence on vegetation development (Odasz 1994; Zmudczyńska et al. 2008,

254   2009; Zmudczyńska-Skarbek et al. 2013). On King George Island we found that, with

255   increasing distance from bird colony edges through successive vegetation zones, the

256   concentrations of nutrients and soil conductivity decreased, while pH increased. These results

257   confirm in detail previous studies that have recognized that the presence of the seabird

258 colonies leads to strong gradients in soil chemistry. Ryan and Watkins (1989) described a

259 similar relationship near snow petrel nest concentrations in continental Antarctica and, in the

260 High Arctic, tundra fertilization was much greater close to colonies, and gradually decreased

261 along the colony-sea axis (Zwolicki et al. 2013; Ziółek and Melke 2014). High concentrations

262 of mineral forms of phosphorus and nitrogen have been reported in surface waters draining

263 from penguin breeding areas close to the location of the current study (Tatur and Myrcha

264 1983), consistent with the values measured here. We recorded the highest values of soil

265 moisture in the central zones of the transects (PD and D zones). These data clearly imply that

266 the differences in structure and composition of the distinct vegetation zones identified are

267 likely to result from the interplay of multiple soil parameters (cf. Webb 1954).

268 Along the gradient in physical and chemical soil properties, we identified five distinct

269 vegetation zones which were similar to those described by Smykla et al. (2007) in a study

270 performed near a single gentoo penguin colony. With this characteristic zonation also being

271 formed near Adélie penguin and giant petrel colonies, we consider that it may represent a

272 general feature for different seabird species. The consistency of the vegetation pattern along

273 the different transects may be in part a consequence of the small number of available plant

274 taxa, giving a limited number of possible combinations, and also could reflect the reaction of

275 the phytocoenosis reaction to direct disturbance caused by seabirds. Rapid nutrient inflow in

276 the vicinity of bird colonies creates imbalanced communities, reflected in the simultaneous

277 presence of pioneer (*P. crispa*) and climax species (*D. antarctica*) (compare with Smith 1972;

278 Convey 1996). Phytocoenosis stabilization occurs with the separation from the strongest

279 influence of a colony, and is evidenced by increasing number of species (MacArthur 1955,

280 Smykla et al. 2007).

281 Adjacent to all three colonies, the closest community consisted only of mats of the

282 nitrophilous foliose alga *P. crispa* overgrowing on over-fertilized habitat with low soil

283   moisture level. This zone is also formed also under extremely variable pH conditions, which

284   could be explained by microbially-mediated guano decomposition processes (Zdanowski et al.

285   2005). The second zone was rich in nutrients and characterized by the highest moisture

286   content and lowest pH, as well as the presence of *P. crispa* and Antarctic hair grass *D.*

287   *antarctica*. The third zone, with *D. antarctica* as a dominant species, is found on moist soil

288   with moderate nutrient levels. The fourth zone was dominated by hydrophilous mosses

289   growing on nutrient-poor habitats, with moderate soil moisture level. The fifth and final zone

290   was covered by an open mixed mesic moss community that is typical of open fellfield habitats

291   in this region (Ochyra 1998), representing the driest and most acidic soil environment.

292   Smykla et al. (2007) noted that the general trend in the change of the vegetation structure

293   between consecutive zones was marked by decreasing abundance of nitrophilous taxa such as

294   *P. crispa*, with the simultaneous appearance and increasing abundance of nitrophobous

295   species of mosses and lichens, therefore postulating that the penguin-derived fertility gradient

296   was a major factor in determining the zonation pattern of vegetation.

297   Bird species differing in diet could potentially have a different impact on soil

298   chemistry, as indicated by the differing effects of fish-eating and planktivorous bird colonies

299   in the Arctic (Zwolicki et al. 2013). In the region of King George Island both penguin species

300   feed primarily on krill (*Euphausia superba*)*,* although gentoo penguins also consume a

301   significant proportion of fish (Volkman et al. 1980). Giant petrels are the main scavenging

302   seabirds in the Antarctic region, relying mainly on penguins, burrowing petrels and krill as

303   reported on South Georgia (Hunter 1983). While such differences in diet could potentially

304   influence soil physico-chemical properties and consequently the zonation in vegetation cover,

305   there was no evidence for this occurring in our study Physical and chemical soil parameters

306   did not differ significantly between the colonies, regardless of the clear gradients along the

307   transects. This could be explained by the plasticity of giant petrel feeding strategies, where

308   males and females can exploit different food resources during chick incubation: males

309   scavenging on beaches and females foraging at sea mostly on krill, squid and fish (Hunter

310   1983). However, males also have the capacity to switch search modes and forage at sea

311   (Gonzales et al. 2000; Forero et al. 2005). It is plausible that on King George Island the

312   proportion of crustaceans, especially krill, in the giant petrel diet was larger than that reported

313   in previous studies from South Georgia, and thus more similar to the two penguin species

314   studied here. However, there were some more subtle differences in the mean cover values of

315   specific plant taxa between the Adélie penguin colony and those of the other species, most

316   apparent in the higher cover values of *P. crispa* and lower average cover of *D. anatarctica*

317   and mosses. Thus, the largest colony (Adélie penguin) had the strongest effect on vegetation.

318   This study clearly demonstrates the significance of bird-derived nutrient enrichment to

319   vegetation development. We found significant composition differences between successive

320   vegetation zones, which were related to the clear differences in physical and chemical soil

321   properties along gradients commencing at the colony edges. The pattern of vegetation

322   zonation was independent of bird species and colony size.

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504   Table captions

505   Fig. 1. Location of transects in the study area. Tr-A1, A2, A3, - transects from Adélie penguin
506   (*Pygoscelis adeliae*) colony; Tr-Pt1, Pt2 - transects from southern giant petrel
507   (*Macronectes giganteus*) colony; Tr-G1, G2 – transects from gentoo penguin
508   (*Pygoscelis papua*) colony (map by Pudełko 2002).

509

510   Fig. 2. Diagram of two way indicator species analyses (Twinspan) based on vegetation
511   composition. P- *P. crispa* zone, T – trampling zone, PD - *D. antarctica* and *P. crispa*
512   zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML -
513   xerophilous moss and lichen zone. Numbers of plots presented for each group/division.

514

515   Fig 3. MDS plot showing ordination of samples based on the identified vegetation zones and
516   colony types. P- *P. crispa* zone, PD - *D. antarctica* and *P. crispa* zone, D - *D.*
517   *antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous
518   moss and lichen zone.

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520   Fig.4. Physical and chemical soil parameters in each vegetation zone. Significant differences
521   (p<0.01) between zones are indicated by lines. Log_{10} transformation for NH_4^+, NO_3^-,
522   NO_2^-, PO_4^{3-} and K^+ data performed for better data visualization. P - *P. crispa* zone, PD -
523   *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and
524   *D. antarctica* zone, ML - xerophilous moss and lichen zone.

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Table 1. Mean and relative ground cover (%) of taxa and ecological groups in the successive vegetation zones identified. P- *P. crispa* zone, T – trampling zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone.

Taxon/ ecological group	Vegetation zones											
	P N = 163		PD N = 53		D N = 95		MD N = 144		ML N = 59		T N = 54	
	Mean	Relative	Mean	Relative	Mean	Relative	Mean	Relative	Mean	Relative	Mean	Relative
P. crispa	7.3	100	2.9	40.6	4.8	13.9	2.3	5.6	0.8	1.7	4.1	52.3
D. antarctica		0.0	4.2	59.4	22.1	63.6	10.5	25.3	9.9	21.5	1.7	21.3
C. quitensis		0.0		0.0	1.5	4.3	0.4	1.0	6.2	13.4		0
Hygrophilous mosses		0.0		0.0	3.8	11.0	23.4	56.2	11.5	24.9	2.1	26.4
Xerophilous mosses		0.0		0.0	1.8	5.2	4.1	9.7	14.3	31.0		0
Usnea sp.		0.0		0.0	0.7	2.0	0.9	2.1	3.4	7.5		0

Table 2. Median values and first and third quartiles (IQ - 25%, IIIQ - 75%) of measured physical and chemical parameters of soil in the identified vegetation zones. P- *P. crispa* zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone.

Soil parameters		Vegetation zones				
		P	PD	D	MD	ML
NH_4^+ (mg kg^{-1})	Median	58.0	10.4	7.9	1.5	1.2
	IQ	24.0	4.4	1.7	0.6	0.9
	IIIQ	582.3	17.3	27.3	12.0	1.8
NO_3^- (mg kg^{-1})	Median	192.3	80.4	51.9	12.3	2.7
	IQ	58.2	37.7	1.7	4.2	1.0
	IIIQ	393.1	202.8	123.5	23.2	5.5
NO_2^- (mg kg^{-1})	Median	4.6	0.8	1.2	0.3	0.1
	IQ	1.4	0.3	0.1	0.2	0.1
	IIIQ	12.7	6.7	2.8	0.7	0.2
PO_4^{3-} (mg kg^{-1})	Median	521.5	166.3	51.6	6.4	8.5
	IQ	119.2	144.8	12.0	3.9	1.5
	IIIQ	1605.4	294.1	280.7	72.0	14.3
K^+ (mg kg^{-1})	Median	309.5	60.8	40.6	24.6	19.4
	IQ	163.2	34.2	20.8	10.7	16.4
	IIIQ	1769.1	90.7	164.7	69.3	27.0
Soil moisture (%)	Median	22.7	33.2	32.3	21.4	15.5
	IQ	18.3	23.4	14.6	15.5	13.7
	IIIQ	31.1	55.9	51.9	57.1	19.2
pH	Median	4.2	4.1	4.4	4.8	5.4
	IQ	3.9	4.0	4.0	4.1	5.2
	IIIQ	6.8	4.2	4.7	5.1	5.6
Conductivity (µS cm^{-1})	Median	840.7	267.2	196.1	83.2	61.7
	IQ	334.2	182.4	115.0	60.1	55.0
	IIIQ	2438.0	341.4	291.1	98.4	104.0

Table 3. SIMPER analysis of vegetation composition between the studied bird colony types.

Taxon/ ecological group	Average cover %			Adélie vs Petrel		Adélie vs Gentoo	
	Adélie	Petrel	Gentoo	Average dissimilarity	Contribution %	Average dissimilarity	Contribution %
Hygrophilous mosses	7.7	51.6	31.72	23.85	47.08	19.08	35.38
D. antarctica	14.8	21.88	19.41	13.56	26.77	17.2	31.88
P. crispa	11.91	3.72	5.45	10.37	20.47	14.35	26.61
Xerophilous mosses	0.24	18.14	8.66	2.59	5.11	2.99	5.54
C. quitensis	0.01	3.27	1.36	0.14	0.29	0.18	0.34
Usnea sp.	0.08	1.23	0	0.14	0.28	0.14	0.25
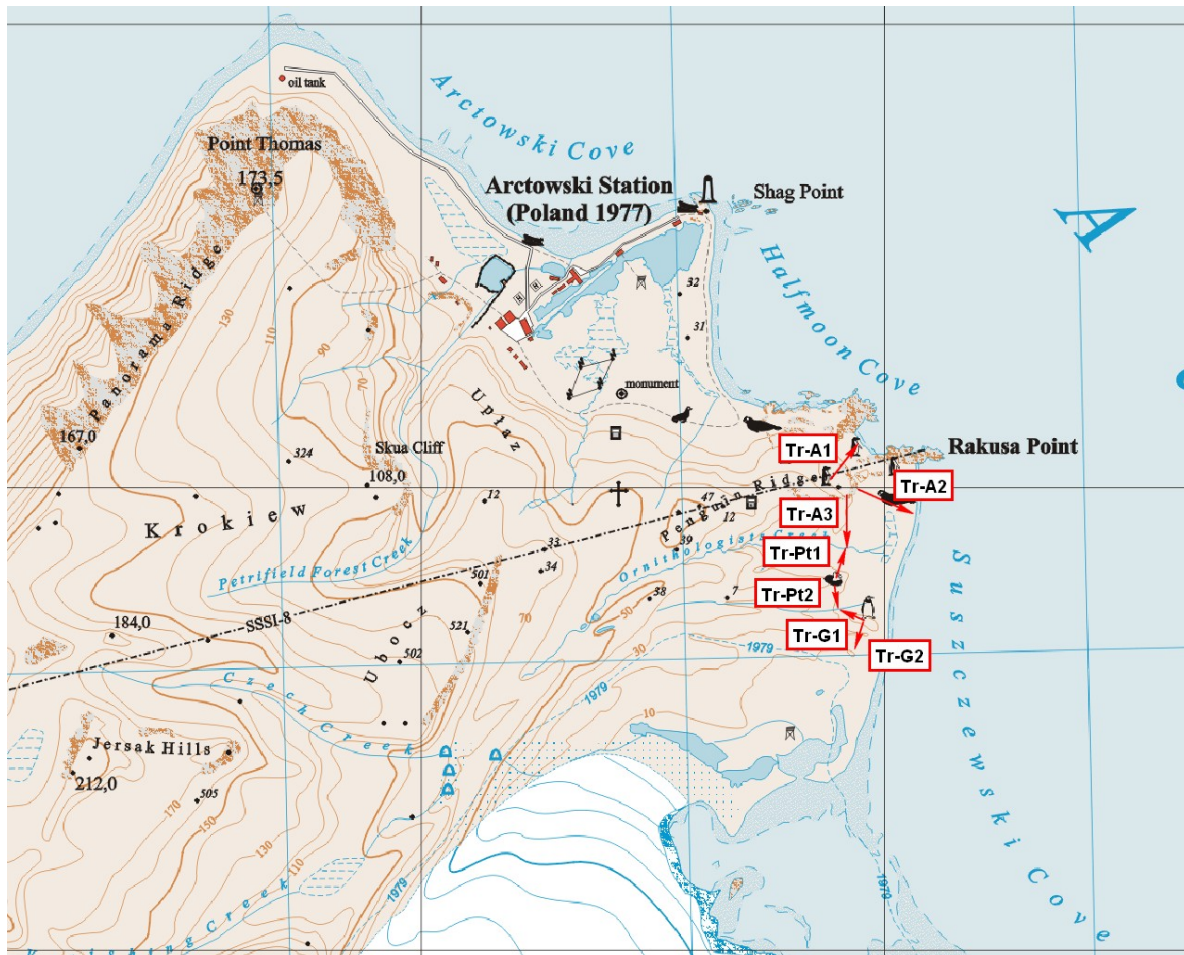
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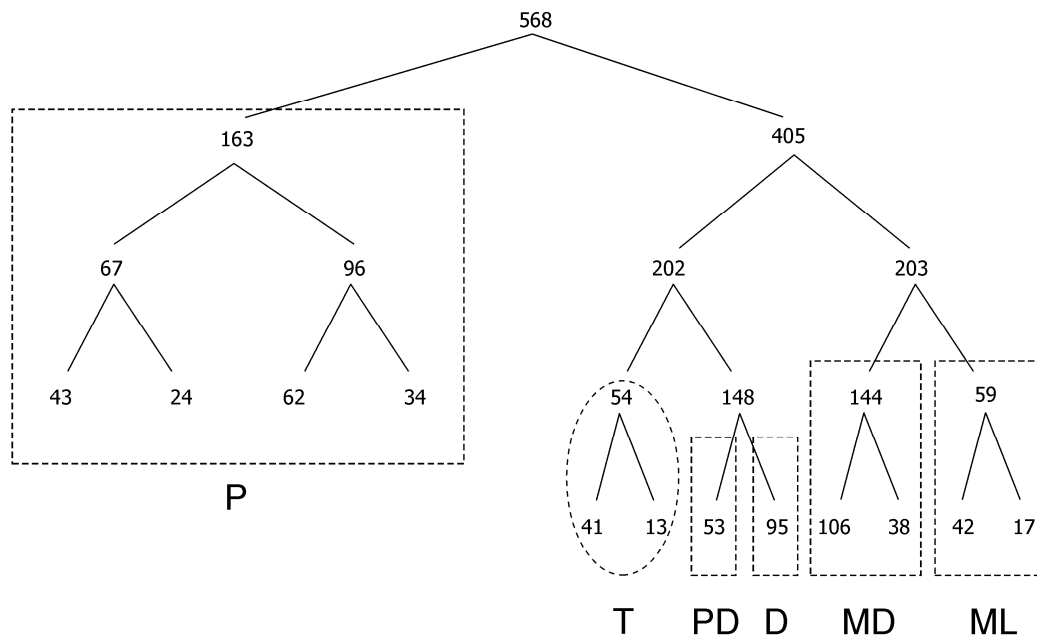
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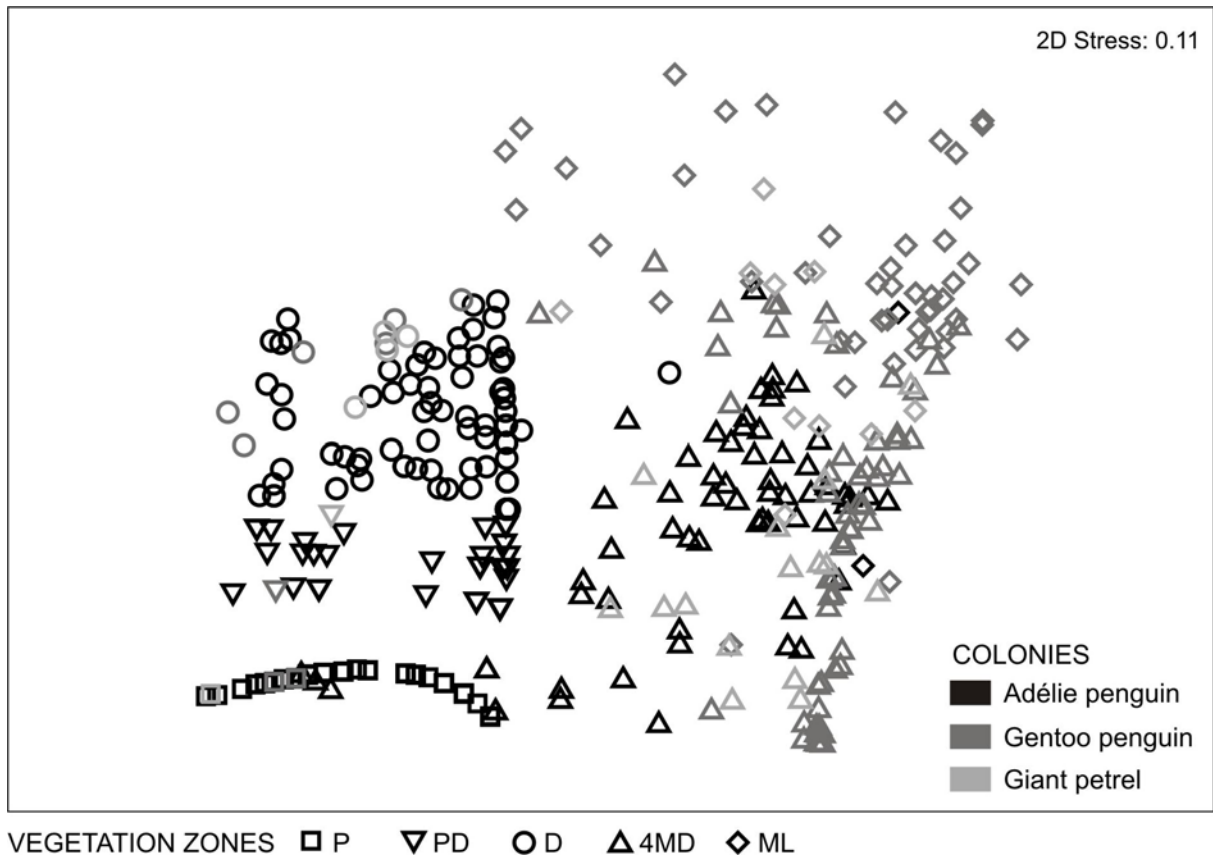
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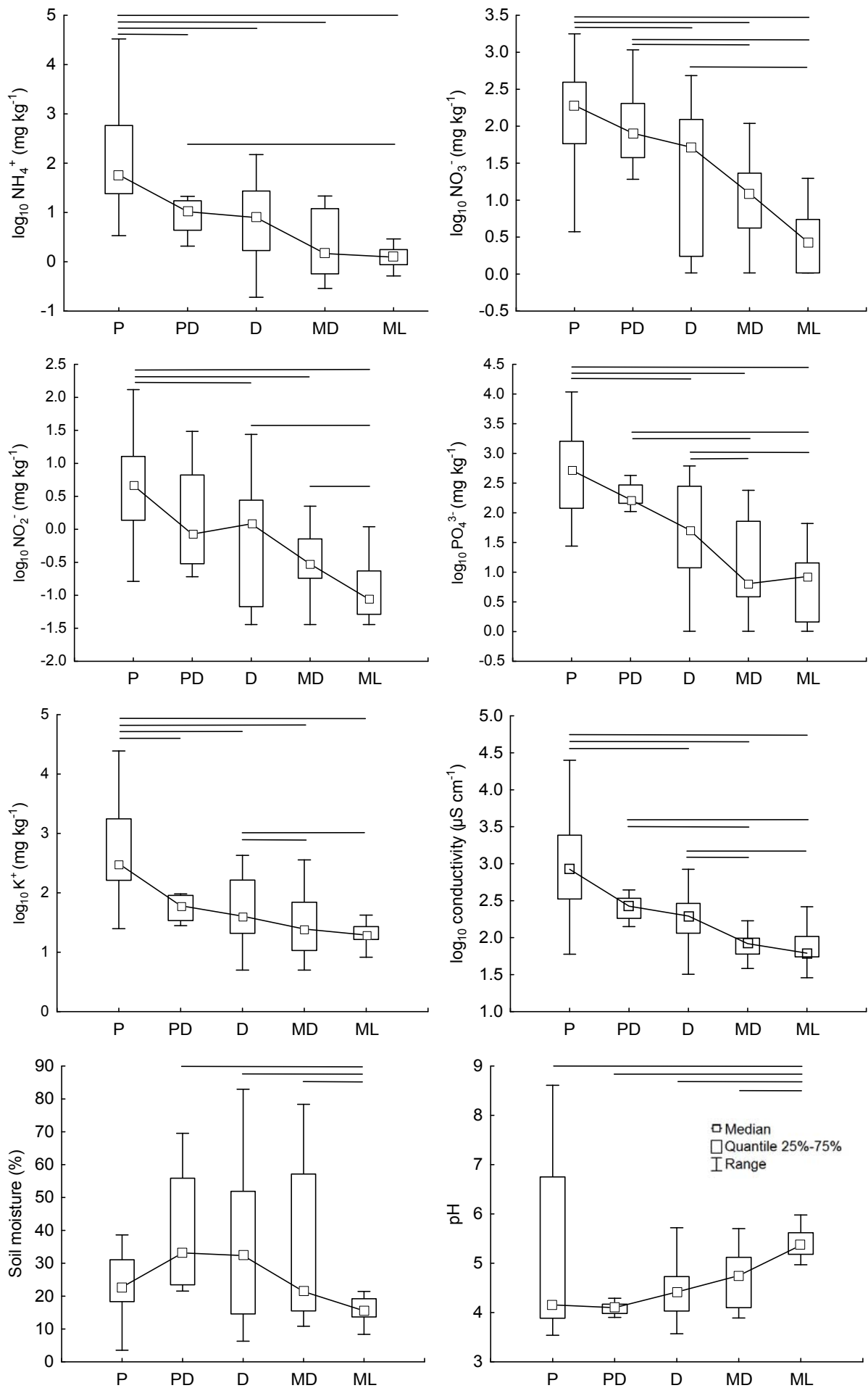
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